Litter decomposition in a cool temperate deciduous forest

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Amounts of autumn tree leaf litter fall, understory litter input, tree leaf litter nutrient input, and rates of dry weight loss in decomposing leaf litter were estimated in an aspen woodland (*Populus tremuloides* Michx. – *P. balsamifera* L.) site in the Rocky Mountains in southwestern Alberta. Tree leaf litter input amounted to 250 g m^{-2} and comprised 3.7% of the total organic matter in the ecosystem (1.92×10^5 kg ha^{-1}). The ratio of the weight of aspen leaf fall to balsam leaf fall was about 6:1. The tree leaf litter input and the total litter input figures were similar to those for other Northern Hemisphere aspen forests. The understory litter input in the study plots was measured as 99 g m^{-2}. The importance by weight of some of the nutrients returned to the soil via tree leaf litter fall was Ca > N > K > Mg > P > Zn > Fe > Mn > Na > Cu. The total weight of these nutrients returned to the soil was 116 kg ha^{-1}, with N, Ca, and K comprising 89% and Mg and P comprising 9.8% of the total.

The dry weight loss of decomposing aspen and balsam leaves was measured at 1-, 5-, 8-, 12-, 18-, 24-, and 30-month intervals by using 3-mm-mesh litter bags, and at 12-, 24-, 36-, 48-, and 60-month intervals by using 10-mm-mesh bags. Litter-bag mesh size was of little consequence to the rate of dry weight loss for the first 12 months, but subsequent dry weight loss was greater in the 3-mm-mesh bags, which maintained higher, more representative, moisture conditions than did the 10-mm-mesh bags. However, tethered leaves lost 1.7 times more weight over the first 12 months of decomposition than did confined litter. The decay rate decline with time and with the depth of the litter bag in the litter layers, with maximum dry weight loss occurring over the period encompassing the fall freeze, winter, and the spring thaw and runoff. Leaf litter placed on north-facing slopes was characterized by significantly slower decay rates than that on south-facing slopes.

The dry weight loss for aspen leaf litter was 26.2 ± 2.0% after 12 months, 40.0 ± 1.6% after 30 months, and 58.7% after 60 months (by regression): for balsam litter it was 21.2 ± 1.9% after 12 months, 37.4 ± 1.7% after 30 months, and 47.9% after 60 months (by regression). The highly leachable component of leaf litter was estimated at 23.1% for aspen and 21.4% for balsam. The time required for 99% decomposition was calculated as about 24 years for aspen and about 27 years for balsam, which gives average annual decay rates of 3.2% for aspen and 2.9% for balsam. The decay rate for *Populus* leaf litter was lower than that for aspen in Alaska and appeared to fit the range for deciduous leaf litter from some forested IBP Tundra Biome sites.

Introduction

The annual litter fall, as it is decomposed, forms the major source of energy and nutrients for the soil and litter organisms of the deciduous woodland. Much attention has recently been paid to techniques devised for studying decomposition of litter (particularly leaf litter) and to rates of decomposition of different types of plant litter in different climatic zones (Edwards and Heath 1963; Weigert and Evans 1964; Witkamp 1966; Howard 1967; van Cleve 1971; Anderson 1973*b*; Gosz *et al.* 1973; Heal and French 1974; Howard and Howard 1974; Jensen 1974; Suffling and Smith 1974; Wood 1974). However, there is still a dearth of information defining the roles of various groups of organisms in the decomposition of litter and nutrient cycling.

The aims of this paper are to quantify aboveground litter input and leaf litter nutrient input, to analyze variations in rates of decomposition because of plant species differences, site aspect, different methods of litter confinement, and varying mesh sizes of the litter bags, and to discuss litter decomposition models and accumulation of soil organic matter in a cool temperate deciduous woodland on the eastern slopes of the Rocky Mountains of Alberta, Canada.

These studies of leaf litter decomposition rates and of nutrient change in decomposing leaf litter (Lousier and Parkinson, unpublished) provide baseline data for an integrated series of projects designed to investigate the roles of various groups of litter and soil organisms in decomposition processes, and the interactions between such groups of organisms in the aspen

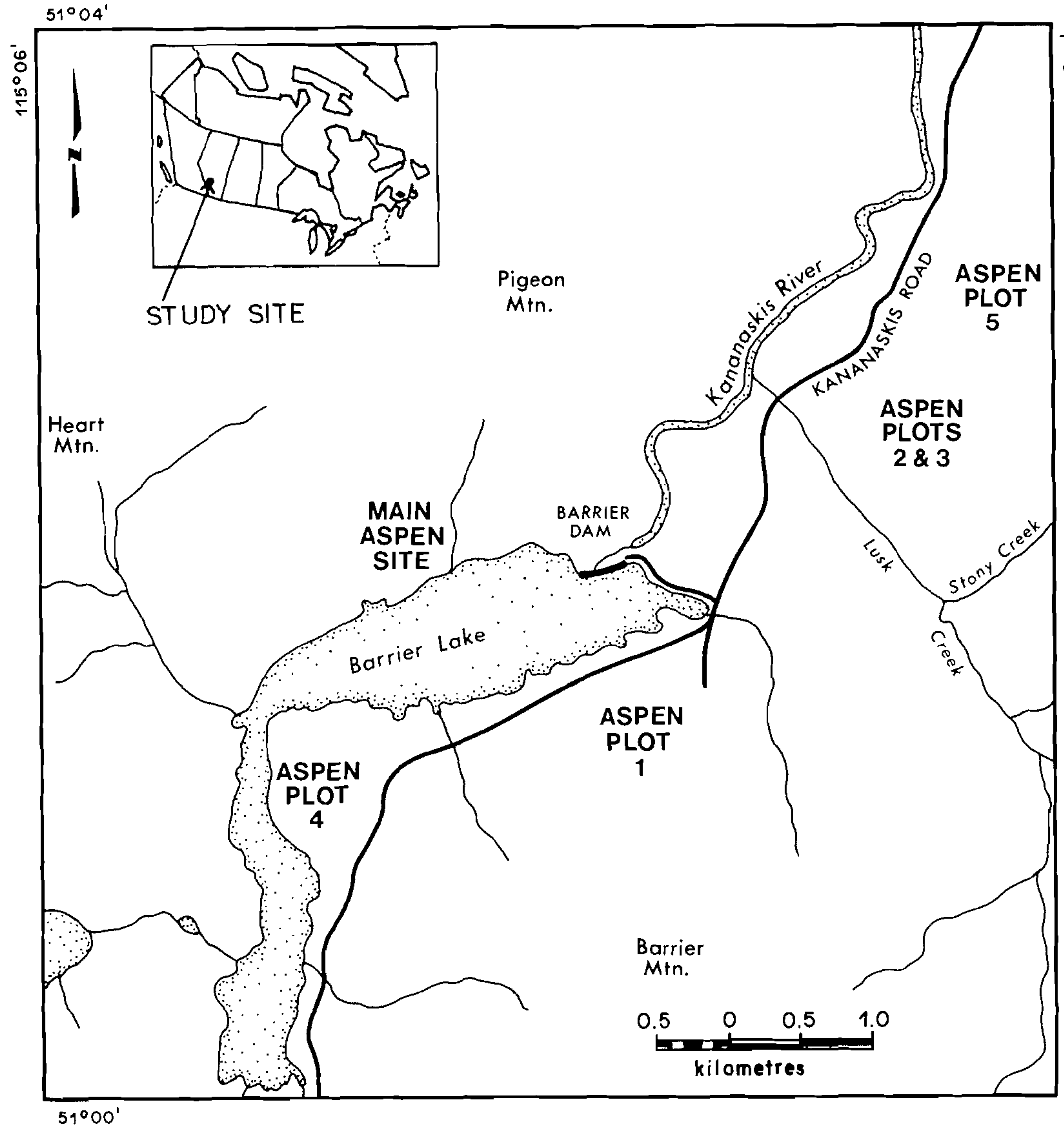

FIG. 1. Location of the main study site and the auxiliary study plots in the Kananaskis Valley.

woodland site which is described below (Dash 1970; Parkinson 1971; Dash and Cragg 1972*a*, 1972*b*; Mitchell 1973; Lousier 1974*a*, 1974*b*, 1975; Carter and Lousier 1976; Lousier and Elliott 1975; Parkinson and Lousier 1975; Mitchell and Parkinson 1976*a*, 1976*b*; Visser and Parkinson 1975*a*, 1975*b*).

Site Description

The main study site was a cool temperate aspen woodland at 1400 m in the front range of the Rocky Mountains, Alberta, Canada (51°2′ N, 115°4′ W) (Fig. 1). The woodland was on a well-drained, south-facing slope at the mouth of the Kananaskis Valley. The climate of the region was essentially continental, characterized by short, dry summers and relatively long, cold winters with intermittent warm chinook winds.

The soil has been classified in the orthic gray luvisol subgroup, and has a surface organic horizon that is easily separated into L, F, and H layers. The soil is frozen from early November to mid-April and has a continuous snow cover from mid-December to mid-April. Soil moisture is near or above field capacity during the period of snowmelt and heavy precipitation (spring), but from mid-July to mid-September it declines almost to the permanent wilting point. Data on various soil and atmospheric conditions for the site are summarized in Figs. 2 and 3.

The tree layer of vegetation is dominated by trembling aspen (*Populus tremuloides* Michx.); balsam poplar trees (*P. balsamifera* L.) are less frequent in occurrence. The understory was composed mainly of various grasses and herbs (*Bromus* sp., *Danthonia* sp., *Agropyron* sp., and *Thalictrum venulosum* Trel., *Heracleum lanatum* Michx., *Epilobium angustifolium* L.), and *Rosa acicularis* Lindl. and *R. woodsii* Lindl. More details on the soil and vegetation of the area were given in Dennis (1970), Parkinson (1971), and Lousier (1974*a*).

Five other aspen stands with north or northwest exposures were selected as auxiliary plots (Fig. 1). These plots were completely deciduous and were as similar as possible to the main aspen woodland plot in terms of tree density, type, age, and species of understory vegetation. Plots 1 and 4 were wholly aspen stands while plots 2, 3, and 5 had some balsam poplar interspersed with the aspen.

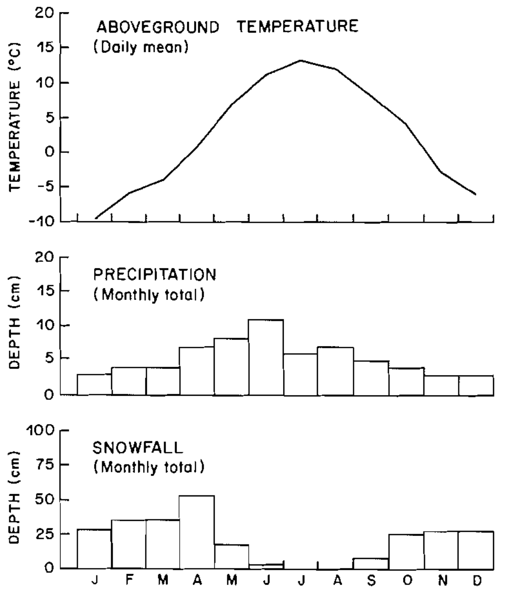

FIG. 2. Monthly means of aboveground temperatures (1 m above litter surface) and total precipitation at the Kananaskis Forest Experimental Station, 1939–1970 (summarized from Kirby 1973).

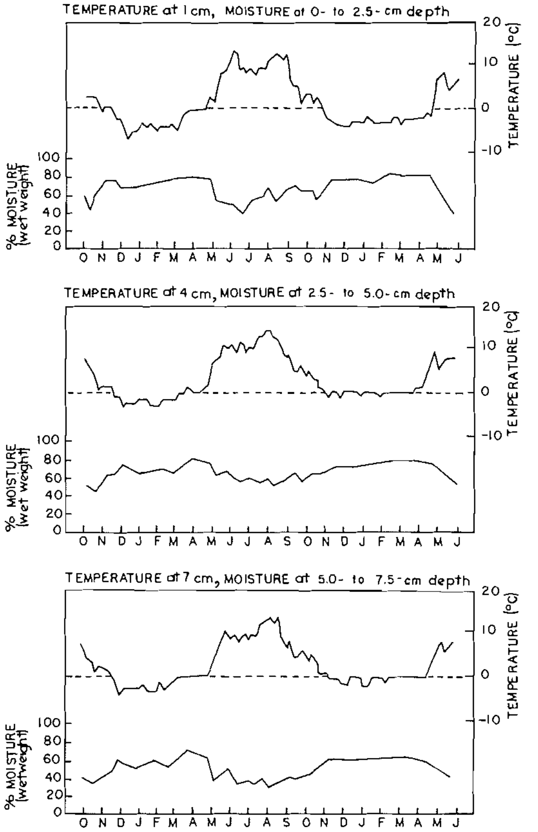

FIG. 3. Summary of seasonal litter and soil temperatures and moisture contents in the aspen woodland (adapted from Mitchell 1974).

Methods

1. Leaf Litter Input

Twelve litter traps were randomly placed in the main study area for the duration of the study period (2 years). These traps were plastic garbage containers (0.167 m^2 surface area) lined to half of their depth (about 40 cm) with plastic bags that were perforated to allow the drainage of rainwater and melting snow. Collection of leaf litter only was made each year daily during the period of maximum litter fall. This period extended over 14–21 days each year, and on only one occasion did the leaves have to be picked from snow. The leaves from each daily collection were oven-dried (80 °C for 48 h) and weighed, and subsamples were analyzed for C, H, N, Ca, Mg, K, Na, Zn, Mn, Cu, Fe, and P. Dried, mill-ground samples were analyzed on a CHN analyzer (Hewlett-Packard, model 185) for the total carbon, hydrogen, and nitrogen. Separate dried, mill-ground samples were acid-digested (nitric acid – perchloric acid) and were used for the determination of Ca, Mg, K, Na, Zn, Mn, Cu, and Fe by atomic absorption spectrophotometry (Perkin-Elmer, model 303) and for the determination of total phosphorus by the molybdenum blue method.

Estimates of amounts of understory litter (grasses, herbs, and shrubs) input were made over 2 years by clipping the ground flora at the soil surface in each of 12 random 1-m^2 plots in August, after the period of maximum aboveground standing crop. These clippings were oven-dried (80 °C, 48 h), and dry weights were calculated.

2. *Leaf Litter Decomposition*

Two sets of tree leaf litter decomposition experiments were carried out: a long-term (5-year) study and a short-term (2.5-year) study. For both of these two groups of experiments, leaves of aspen and balsam were caught in aboveground nets, air-dried to a constant weight for 3 weeks (at 21 °C), enclosed in litter bags, and placed in field plots in the study site(s).

Long-term Litter Decomposition

The litter bags used in this experiment were 10-mm-mesh, large-size nylon hairnets, which when filled with leaves, assumed the size and shape of the volume of leaves enclosed. The leaves collected (as described above) were placed in the hairnets, with 100 leaves (0.046 ± 0.008 g per leaf, $P = 0.05$) per hairnet for aspen and 25 leaves (0.188 ± 0.022 g per leaf, $P = 0.05$) per hairnet for balsam. In each of the years 1966, 1967, 1968, 1969, and 1971, 100 bags of leaves were made up for aspen; the same procedure was followed for balsam except that no bags were made up in 1968. In each of the years, a random sample of 10 bags was taken from each set of 100 and oven-dried at 80 °C for 48 h, and an ovendry weight correction factor was determined (Table 1). Each litter bag in this random sample was then placed in a paper bag, transported to the field sites, placed on the litter surface, picked up and replaced in the paper bag, and returned to the laboratory to determine the amount of leaf drop-out and the spillage correction factor (Table 1). These bags were then returned to the original sets of 100 for distribution in the field. In 1966, 1967, and 1968, each yearly complement of litter bags was then placed in among the freshly fallen litter in the main aspen site 3–4 weeks after leaf fall; each bag was tethered to a separate, numbered stake. In each of 1969 and 1971, the 100 bags of aspen leaves were distributed, in sets of 10, among 10 different plots (5 in the main aspen study area and 5 in auxiliary aspen stands (see Fig. 1)) to measure within- and between-site variation in dry weight loss. Table 2 outlines the number of samples taken each year of sampling.

To compare decomposition rates and movement of litter into the organic layers of the forest floor, 100 individual balsam leaves were tethered with nylon thread to numbered stakes and were placed in the vicinity of the 100 bags of balsam leaves in 1971 (only balsam leaves were tethered individually because of their more robust nature). Twenty of these leaves were sampled in 1972, and to avoid errors due to breakage from sampling, only whole leaves were used to determine dry weight loss. An attempt was made in 1973 to retrieve more of these leaves, but it appeared that the leaves had separated from their petioles and could not be found.

TABLE 1. Ovendry weight and spillage correction factors (%) for leaf litter in 10-mm-mesh bags (±95% confidence limits)

	Ovendry weight correction	Spillage	Correction
		Mean	Range
Aspen	23.0±3.8	4.2±2.3	0.8–10.9
Balsam	12.5±3.4	3.8±2.1	1.7– 9.4

TABLE 2. Times of placement and sampling of litter bags

	Year put in field	Number of bags sampled per year		
		1969	1971	1972
Aspen	1966	10	10	—
	1967	10	10	10
	1968	10	10	10
	1969	—	100	—
	1971	—	—	100
Balsam	1966	10	10	—
	1967	10	10	10
	1969	—	10	10
	1971	—	—	10

Short-term Decomposition

This project was set up to examine dry weight loss in the initial stages of leaf litter decomposition. The litter bags used were of 3-mm nylon mesh, 20 cm × 20 cm in size. The 3-mm mesh size was chosen to minimize leaf drop-out but was large enough to allow passage through by fauna.

The leaves collected in aboveground nets were air-dried for 2 weeks, placed in the litter bags, and air-dried for an additional week. One hundred bags each of aspen (10.5 ± 0.7 g per bag) and balsam (5.9 ± 0.6 g per bag) were made up; the difference in weight of leaves in the litter bags is due to the difference in leaf size between the two tree species (see above). For each type of litter, 10 bags were taken at random and oven-dried at 80 °C for 48 h, and the ovendry weight correction factor was determined (7.0 ± 1.0% for *P. tremuloides* and 8.2 ± 1.3% for *P. balsamifera*). There was no measurable leaf drop-out from the 3-mm-mesh bags.

The litter bags were placed among the freshly fallen litter in the main field plot about 1 month after leaf fall and 10 bags of each type of litter were sampled at the following intervals after placement in the field: 1 month, soil frozen, light snow cover, late fall; 5 months, soil thawed, free of snow, early spring; 8 months, early summer; 12 months, midfall, soil beginning to freeze; 18 months, early spring; 24 months, midfall; 30 months, early spring. At each sampling time, the retrieved bags were returned to the laboratory, extraneous material was removed, and the wet weight of the leaf material was measured. The material was reweighed after oven-drying at 80 °C for 48 h.

Results

1. *Leaf Litter Input*

A summary of the aboveground litter input for

TABLE 3. Aboveground litter input and biocontent data for the aspen woodland

	Litter input, g dry wt. m^{-2}	Caloric input, kcal m^{-2}	Carbon input, g dry wt. m^{-2}
Tree litter			
Aspen leaves	215±40[a]		106
Balsam leaves	35±15		18
Total tree leaf litter	250±49	1180[c]	124[f]
Non-leaf litter[b]	66	308[d]	32[g]
Total tree litter	316	1488[e]	156
Understory	99±11	465	46[h]
Total litter fall	415	1953	202

[a] Confidence limits of 95%.
[b] Calculated as 21% of total tree litter (Bray and Gorham 1964).
[c] 4.72 kcal g^{-1} (Peterson *et al.* 1970).
[d] 4.69 kcal g^{-1} (Peterson *et al.* 1970).
[e] 4.70 kcal g^{-1} (Newbold 1967).
[f] 48.4% of dry weight of litter.
[g] 48.6% of dry weight of litter.
[h] 46.5% of dry weight of litter.

the study site is given in Table 3. Leaf fall occurred over a period of about 2 weeks in the latter part of September and amounted to 253.9 ± 51.4 g m^{-2} for 1972, and 224.8 ± 81.8 g m^{-2} (Mitchell 1974) for 1973. The mean of 250 g m^{-2} for tree leaf litter input matched the estimate by Bray and Gorham (1964) for cool temperate deciduous forests (because there was no significant difference between the autumnal leaf fall in 1972 and 1973, the mean was determined by grouping together all the weights of all the samples from the 2 years). Various authors have felt that the figure of 21% (Bray and Gorham 1964) for the percentage of non-leaf litter is too low. Andersson (1970), Carlisle *et al.* (1966), Hurd (1971), Kira and Shidei (1967), and Sykes and Bunce (1970) have published estimates of 41, 45, 36, 33–50, and 37%, respectively. Because of the occurrence of high winds at various times of the year and the fact that the aspen association may be a successional stage, the percentage of non-leaf litter may well exceed 21%. The high winds may contribute to a significant input into the litter layers by green leaf fall; this perhaps provides an underestimate of tree leaf litter input. By using the minimum and maximum estimates of Kira and Shidei (1967), non-leaf tree litter in this site would range from 125 to 250 g m^{-2}, total tree litter would range from 375 to 500 g m^{-2}, and the total litter fall would range from 474 to 599 g m^{-2}.

The estimate for understory litter input (99 g m^{-2}) in the present study plots was for a closed canopy; this contrasts with estimates for ground flora under open canopy, which ranged as high as 238 g m^{-2} aboveground primary production (Dennis 1970). The understory litter input figure of 99 g m^{-2} in this study was an underestimate because it did not measure primary production (because of the asynchrony of harvest times and growth phases and because of the exclusion of grazed plant biomass) and did not include the total litter input of shrubby perennial species (e.g. *Rosa* spp.). It is probable that the estimate of 99 g m^{-2} was low by at least 10%, half of which consisted of reproductive structures (Dennis 1970).

Again by using the percentages of Kira and Shidei (1967), annual caloric input would range from 2230 to 2820 kcal m^{-2}, and the annual input of carbon would be 231 to 292 g m^{-2}. Dash and Cragg (1972*a*) calculated a caloric input of 2300 kcal m^{-2}, which compares favourably with the estimates in this study. Hughes (1971*a*, 1971*b*) estimated the caloric input for litter in an alder–birch woodland in northern England as 2450 kcal m^{-2}.

The nutrient content (excluding carbon and hydrogen) of the annual leaf litter fall amounted to 116 kg ha^{-1}. Nitrogen, calcium, and potassium made up 89.0% of the total, and magnesium and phosphorus made up another 9.8% (Table 4). The order of importance, by weight, of the elements was Ca > N > K > Mg > P > Zn > Fe > Mn > Na > Cu, which follows generally the order given by Rodin and Bazilevich (1967)

TABLE 4. Amounts of nutrients returned annually to the soil in the leaf litter fall of aspen and balsam in the aspen woodland

Element	Aspen, kg ha^{-1}	Balsam, kg ha^{-1}	Total, kg ha^{-1}
C	1060.00	179.00	1239.00
H	131.40	19.90	151.30
N	24.00	3.61	27.61
Ca	47.30	8.40	55.70
Mg	5.20	0.91	6.11
Cu	0.01	0.0032	0.013
Fe	0.14	0.032	0.172
K	15.30	4.62	19.92
Mn	0.11	0.02	0.13
Na	0.11	0.01	0.12
Zn	0.50	0.08	0.58
P	4.50	0.77	5.27

for some Russian aspen forests. This order is similar to that given in Gosz *et al.* (1972) for a mature northern U.S. hardwood forest, where, however, N > Ca and K > Mn > Mg.

The weight of nutrients returned through tree litter fall in Russian aspen (*P. tremula*) forests ranged from 250 kg ha^{-1} (Poyarkova 1954) to 239 kg ha^{-1} (Remezov 1956) to 279 kg ha^{-1} (Remezov *et al.* 1959). Gosz *et al.* (1972) measured the nutrient content of tree litter fall in a hardwood forest as 140.4 kg ha^{-1}. The Russian figures included weights of silicon, sulphur, and aluminum, the latter being a trace element, and the American figure included sulphur, which was as abundant as magnesium. If the weights of these additional elements and nutrient input from non-leaf litter were included, the Kananaskis aspen total would perhaps approach or exceed the estimate of Gosz *et al.* (1972).

2. Dry Weight Loss

The losses in dry weight of leaf litter of the two *Populus* species over the first 30 months of decomposition and the calculated decomposition parameters are given in Table 5. During this 30-month period, the dry weight loss for aspen leaf litter in 3-mm-mesh bags was significantly greater ($P = 0.05$) than that for balsam. The most rapid dry weight loss was during the period encompassing fall freezing, winter, and spring thawing, all of these being important times in the release of nutrients from soil organic matter (Bleack 1970; Witkamp 1971; Wood 1974; Parkinson 1975).

Table 6 indicates no significant difference in dry weight loss between the two species of tree leaf litter in 10-mm-mesh bags for the first 36 months. The 60-month data for both aspen and balsam leaf decomposition were from a plot on a north-facing slope (aspen plot 1 (Fig. 1)). The low figure for aspen dry weight loss after 60 months (significantly lower than that for aspen after 48 months) appeared to be substantially explained by the effects of site aspect (Table 7). However, the dry weight loss for balsam leaves after 60 months on the north-facing slope indicated little apparent effect of site aspect on the decomposition rate of balsam leaves.

The dry weight loss after 12 months was the same for litter in 3-mm- and 10-mm-mesh bags, but after 24 months, dry weight loss in 3-mm-mesh bags had reached or exceeded the loss levels attained after 36 months in 10-mm-mesh bags.

The most significant data in Table 6 are the dry weight loss results for tethered balsam leaves after 12 months: the dry weight loss is 1.7 times greater than that for balsam leaves in 10-mm-mesh bags over the same experimental period. Only after 30 months in the field does the balsam litter in the 3-mm-mesh bags approach the 12-month dry weight loss of tethered balsam leaves.

Discussion

1. Leaf Litter Fall and Dry Weight Loss

The accumulation of organic matter on the forest floor represents an energy and nutrient storage pool, a diverse habitat for many different types of heterotrophic organisms, and a substratum for plants. The amount of the accumulation is dependent on litter input, organism successional time, and the rate of decomposition (Olsen 1963). The decomposition rate is, in turn, determined by the nature of the litter input, temperature, moisture, soil type, altitude, and aspect.

Annual litter and nutrient fall must be considered as a dynamic, ever-changing process. Annual and seasonal differences in litter fall, because of climatic fluctuations and (or) changes in vegetative composition and phenology, affect subsequent processes of decomposition, mineralization, and immobilization. Cool temperate forests in North America are usually faced with abundant litter fall for only a very short period during the year and with nutrient flushes in the soil perhaps twice a year, during spring thaw and during autumn litter fall. In the Kananaskis

TABLE 5. Dry weight loss (%) and decomposition parameters for leaf litter decomposition in the aspen woodland (t_0 = 5/11/72) (3-mm-mesh bags)

	Aspen					Balsam				
Decomposition time, months	Dry weight loss, %	k	k'	$t_{0.50}$	$t_{0.99}$	Dry weight loss, %	k	k'	$t_{0.50}$	$t_{0.99}$
1	2.9±0.7[a]	0.307	0.027	2.3	16.3	2.0±0.5	0.240	0.020	3.1	20.8
5	18.3±1.4	0.486	0.183	1.4	10.3	15.3±1.4	0.400	0.153	1.8	12.5
8	23.3±3.1	0.481	0.233	1.8	12.5	19.3±3.0	0.339	0.203	2.1	14.7
12	26.2±2.0	0.303	0.262	2.3	16.6	21.2±1.9	0.283	0.212	2.9	21.1
18	34.7±2.3	0.264	0.347	2.4	17.7	27.6±2.3	0.213	0.276	3.3	23.6
24	36.7±2.0	0.229	0.367	3.1	21.9	34.0±2.7	0.207	0.340	3.4	24.5
30	40.0±1.6	0.205	0.400	3.4	24.4	37.4±1.7	0.187	0.373	3.7	26.7

NOTE: $t_{0.50}$, 50% decomposition time (years); $t_{0.99}$, 99% decomposition time (years); k, $X/X_0 = e^{-kt}$; $k' = 1 - X/X_0$, where X_0 = initial weight of litter (t_0) and X = weight of litter at time t.

[a] Dry weight loss ±95% confidence limits.

TABLE 6. Dry weight loss (%) and decomposition parameters for leaf litter decomposition in the aspen woodland (10-mm-mesh bags and tethered leaves)

	Aspen					Balsam				
Decomposition time, months	Dry weight loss, %	k	k'	$t_{0.50}$	$t_{0.99}$	Dry weight loss, %	k	k'	$t_{0.50}$	$t_{0.99}$
12	25.4±2.7[a]	0.292	0.250	2.4	17.1	23.1±2.5	0.264	0.232	2.6	19.0
						38.1±4.2[b]	0.485	0.384	1.5	10.3
24	27.5±2.0	0.161	0.275	4.3	31.6	29.2±2.0	0.166	0.282	4.6	30.1
36	33.8±2.2	0.141	0.320	5.8	35.5	34.9±2.0	0.153	0.350	5.2	32.7
48	51.8±1.9	0.217	0.518	3.6	23.0	38.0±2.1	0.121	0.380	6.1	41.3
60	40.3±2.0	0.113	0.430	6.3	44.3	47.8±2.2	0.131	0.477	5.5	38.2

[a] Dry weight loss ±95% confidence limits.

[b] Tethered leaves.

aspen woodland, these flushes were coincident with the highest annual levels of soil moisture (Fig. 2) and were reflected in peaks in abundance for those soil organisms with shorter generation times (Dash and Cragg 1972*a*; Visser and Parkinson 1975; M. J. Elliott, personal communication; Lousier, unpublished data).

Table 8 summarizes the annual amounts of tree litter fall in some cool temperate deciduous forests throughout the Northern Hemisphere. Averaging the figures gives an annual leaf litter input of 2.50 × 10^3 kg ha^{-1} and an annual total litter input of 4.10 × 10^3 kg ha^{-1}; the latter figure exceeds considerably the estimate of 3.5 × 10^3 kg ha^{-1} of Bray and Gorham (1964). While the Kananaskis average annual tree leaf litter input (Table 3) compares with the average in Table 8, the average annual total litter input for this site is low.

The concentration of nutrients returned in plant material to the soil is important because of its influence on both the rate of litter decomposition and the amounts of nutrients liberated during decomposition (Jensen 1974). The nutrient content of litter fall is very variable because of a natural variation in nutrient concentrations of plant tissue and of changes in the type and timing of litter fall (Gosz *et al.* 1972). Such variability between sites and between different tree species for the most abundant nutrients is illustrated in Table 9. Obviously the Kananaskis site figures (Table 4) are lower because the nutrient content of only tree leaf litter was measured; however, with total litter nutrient content in mind, the Kananaskis data, with the exception of phosphorus, would fall within the range for *Populus* spp. from Russia.

The data on rates of decomposition of leaf litter of aspen and balsam in comparison with similar data for decomposition of leaf litter

TABLE 7A. Dry weight loss (% ±95% confidence limits) for aspen litter in 10-mm-mesh bags in north- and south-facing plots

	Plot	Decomposition time		
		1 year	2 year	3 year
North-facing slope[a]	1	18.2±2.9	23.7±3.0	27.9±2.8
	2	17.1±2.9	22.7±2.9	26.2±2.6
	3	17.7±2.7	23.1±2.9	27.4±2.6
	4	19.8±2.6	24.7±3.0	28.9±2.5
	5	17.1±2.7	21.9±2.6	27.1±2.5
South-facing slope[a]	1	25.9±2.8	30.5±3.2	34.4±3.0
	2	26.0±3.0	30.8±3.1	34.9±3.1
	3	24.7±2.9	30.2±3.3	33.9±3.1
	4	24.1±3.0	30.1±3.4	35.2±3.2
	5	25.1±3.0	29.4±3.1	36.0±3.1

[a] The north-facing plots are given as aspen plots 1, 2, 3, 4, and 5 in Fig. 1. The south-facing plots were in the main aspen site in Fig. 1.

TABLE 7B. ANOVA summary of above data

Source of variation	Sum of squares	Degrees of freedom	Mean square
Total	869.8	29	
Cells	850.3	5	
Factor A (aspect)	386.6	1	386.6
Factor B (time)	463.5	2	231.8
A × B interaction	0.2	2	0.1
Within cells (error)	19.5	24	0.8

Significance

Aspect: $F_A = 483.3 > F_{0.05(1),1,24} = 4.26$

Time: $F_B = 579.4 > F_{0.05(1),2,24} = 3.40$

Aspect × time interaction: $F_{A \times B} = 0.125 < F_{0.05(1),2,24} = 3.40$

material of a range of deciduous tree species are given in Table 10. These demonstrate, even taking into account the data from Alaska, a generally much lower decomposition rate at the aspen site under present study.

It appears that the 12-month percentage dry weight losses recorded here for *Populus* litter decomposition fall within the range for deciduous leaf litter from some forested sites in the IBP Tundra Biome (Heal and French 1974). Differences recorded in the present study between the decomposition rates of aspen and balsam litter under the same environmental conditions may be ascribed to differences in substrate quality between these two species; however, little work has been done, as yet, on this aspect.

2. *Assessment of Litter Bag Methods for Studying Litter Decomposition*

As in most work on litter decomposition, litter bags were used in the present study. Most workers have assumed that the litter-bag environment is representative of that to which the litter is naturally exposed. However, the bag environment is probably somewhat different from the natural environment simply because of the more homogeneous substrate, and by the alteration of the manner in which litter naturally accumulates. Bocock and Gilbert (1957), Witkamp and Olsen (1963), and Anderson (1973*b*) have reported differences in weight loss between samples confined in litter bags and unconfined leaf samples. Witkamp and Olsen (1963) found a twofold to threefold greater weight loss in unconfined litter. Anderson (1973*b*), on the other hand, maintained that while the results that he obtained were not statistically significant, they were significant biologically in terms of real differences in the feeding activities of soil animals on confined and unconfined litter. The weight loss in tethered

TABLE 8. Annual amounts (in kg ha^{-1} year^{-1} × 10^3) of tree litter fall in some cool temperature deciduous forests throughout the northern hemisphere

Region	Forest tree species	Leaf litter	Total litter	Reference
Canada	*Populus* spp.	1.00–2.04		Coldwell and DeLong 1950
	Betula populifolia Marsh.	1.03–2.34		Coldwell and DeLong 1950
	Fagus grandifolia Ehrh.	1.69–2.10		Coldwell and DeLong 1950
	Acer saccharum Marsh.	2.17–3.62		Maldague 1967
	A. saccharum – *Quercus* spp.	3.1	4.3	Bray 1963
	Alnus rugosa		5.5	Daly 1966
United States	*Alnus rubra* Bong.	3.46–6.39	4.49–9.90	Zavitkovski and Newton 1971
	A. rubra	4.22	4.91–5.59	Gessel and Turner 1974
	A. crispa spp. *sinuata* (Regel) Hult – *Salix* spp.	1.82–1.84	2.26–2.95	Hurd 1971
	Populus balsamifera ssp. *trichocarpa*	1.49–1.86	2.39–3.45	Hurd 1971
	Alnus incana		1.63–2.14	van Cleve *et al.* 1971
	Acer saccharum, *F. grandifolia*, *Betula allegheniensis* Britt.	2.80	5.70	Gosz *et al.* 1972
U.S.S.R.	*Populus* spp.		4.60–6.00	Sviridova 1961
	P. tremula L.		3.90–4.90	Remezov and Bykova 1953
Hungary	*Populus alba* L.		3.5–4.6	Járó 1958
	P. nigra L.		4.0	Járó 1958
	Populus sp.		4.4	Járó 1958
	Alnus glutinosa (L.) Gaetn.		3.3	Járó 1958
England	*Quercus petraea* (Mattuschka) Liebl.	2.13	3.86	Carlisle *et al.* 1966
	Fagus sylvatica L., *Castanea sativa* Mill	3.58	4.25	Anderson 1973*a*
	Alnus glutinosa, *Betula pendula* Roth.	1.85	2.63–2.73	Hughes 1971*a*
	Q. petraea, *Q. robur* L., *Fraxinus excelsior* L.	3.23	5.13	Sykes and Bunce 1970
	Betula spp.	0.94–1.27	1.50–1.80	Viro 1955
	Fagus sylvatica	3.57	5.70	Nihlgard 1972
	Quercus robur	3.26	5.28	Andersson 1970
	Populus tremula	1.90	3.94	Andersson and Enander 1948
	F. sylvatica	2.79	3.94	Nielson, B.O. (quoted in Jensen 1974)
	F. sylvatica	2.14–2.54	2.99–4.01	Gossuin 1974
	F. sylvatica		2.40–5.00	Delecour *et al.* 1967
	F. sylvatica		4.4	Nanson 1962
	F. sylvatica		4.2–4.4	Duvigneaud *et al.* 1972

TABLE 9. Comparison of amounts of nutrients (kg ha^{-1} year^{-1}) returned to the soil in litter fall in deciduous tree species of some cool temperature woodlands

Forest tree species	N	P	K	Ca	Mg	Reference
Alnus rubra	30.9	1.7	13.0	—	—	Tarrant 1964
A. rubra	112.3	—	—	—	—	Tarrant *et al.* 1969
Betula spp.	30–34	7.9–9.2	22.4–26.6	24.9–47.7	11.4–14.2	Remezov and Pogrebnyak 1969
Quercus petraea	41.06	2.19	10.51	23.83	3.87	Carlisle *et al.* 1966
Fagus sylvatica	69	5.0	14.4	31.7	4.3	Nihlgard 1972
F. sylvatica	33.5	1.7	8.5	33.4	5.18	Nielson, B.O. (quoted in Jensen 1974)
Populus spp.	31–54	3.5–4.4	22.4–84.7	66.0–105.1	9.9–14.2	Remezov and Pogrebnyak 1969
Acer saccharum – *F. grandifolia* – *B. allegheniensis*	52.7	3.6	17.7	39.7	5.5	Gosz *et al.* 1972

TABLE 10. Comparison of k values for a range of deciduous litter (in some cases these have been calculated from the literature data)

Site	Tree species	k	$t_{0.50}$, years	Reference
Blean Woods, England	*Castanea sativa*	0.406–0.623	1.1–1.7	Anderson 1973*b*
	Fagus sylvatica	0.218–0.327	2.1–3.2	Anderson 1973*b*
Fontainebleau	*Fagus sylvatica*	0.520–0.230	1.3–3.0	Lemée and Bichaut 1973
	Quercus petraea	0.533	1.3	Lemée and Bichaut 1973
	Carpinus betulus	0.910	0.8	Lemée and Bichaut 1973
Alaska	*Betula papyrifera*	0.456	1.5	van Cleve 1971
	Populus tremuloides	0.389	1.8	van Cleve 1971
	Alnus crispa spp. *sinuata*			
	in *B. papyrifera*	0.408	1.7	van Cleve 1971
	in *P. tremuloides*	0.423	1.6	van Cleve 1971
Hubbard Brook, New Hampshire	*Acer saccharum*	0.510	1.4	Gosz *et al.* 1973
	Fagus grandifolia	0.370	1.9	Gosz *et al.* 1973
	Betula allegheniensis	0.850	0.8	Gosz *et al.* 1973
Oak Ridge, Tennessee	*Liriodendron tulipifera*	0.852	0.8	Ausmus and Witkamp 1974
	Fraxinus pennsylvanica	0.768	0.9	Ausmus and Witkamp 1974
	Carya tomentosa	0.788	0.88	Ausmus and Witkamp 1974
	Quercus spp.	0.707	0.98	Ausmus and Witkamp 1974
	Acer rubum	0.883	0.78	Ausmus and Witkamp 1974
	Cornus florida	1.152	0.6	Ausmus and Witkamp 1974
Kananaskis	*Populus tremuloides*	0.113–0.486	1.4–6.3	This study
	Populus balsamifera	0.121–0.485	1.5–6.1	This study

leaves due to breaking and (or) greater faunal comminution can be greater and lead to an overestimation of the rate of decomposition, but by being mixed with other natural litter, tethered leaves can be a part of a more nutrient diverse and more decomposable (in terms of the decomposers) substrate. Witkamp and Olsen (1963) found that litter material confined in litter bags usually had a higher moisture content than unconfined litter, which could mean accelerated decomposition rates in confined litter, but in litter bags of different mesh sizes, Anderson (1973*b*) found no differences in litter moisture content. However, the evidence in Table 11 indicates that moisture content of litter can vary with the method of confinement and the litter type.

The mesh size can also be an important factor in soils that have higher degrees of faunal comminution of litter (Gilbert and Bocock 1962). Small mesh excludes larger fauna which can be important in the decomposition and nutrient cycling process (Edwards and Heath 1963). On the other hand, large mesh size may promote physical loss of material that is not yet decomposed (Table 1) (van Cleve 1971; Suffling and Smith 1974). Litter bags also artificially maintain the litter on the surface and within the organic layers and thus may not reflect true patterns of litter movement within the organic layers and down the soil profile.

Techniques involving confinement of litter have some advantages, however. Enclosing samples enables their recovery with some guarantee of being intact. The chance of physical loss of undecomposed material can be reduced so that a reasonably accurate determination of weight loss and chemical change can be made. Also, by altering the mesh size of the bag, effects of different-sized litter and soil fauna on decomposition can be compared (Edwards and Heath 1963).

In this project, the short-term study was begun after the completion of the long-term investigation. Based on some observations on the use of 10-mm-mesh hairnets for litter bags (i.e., the hairnets tended to get hung up on vegetation, and after 3 years, many bags were still exposed; there were significantly lower moisture contents in the confined litter throughout the study; the leaves inside the nets became balled-up and matted in an artificial fashion; the bags sank unevenly into

TABLE 11A. Moisture contents of litter in 3-mm-mesh litter bags, unconfined litter, and the surrounding organic matter (±95% confidence limits)

Months	Litter bag, aspen	Litter bag, balsam	Loose litter	A_0L layer
1	24.1±3.5	25.7±3.2	29.1±3.1	55.1±2.7
5	63.1±2.7	62.1±2.8	49.5±2.7	58.9±2.7
8	16.8±3.0	20.1±3.6	32.4±3.0	40.3±3.0
12	48.4±2.7	58.9±3.0	46.5±2.8	59.1±2.9
18	43.0±2.5	42.1±2.8	45.0±2.3	53.2±2.2
24	32.3±2.7	38.7±2.7	32.0±2.9	55.0±2.7
30	44.2±2.6	43.1±2.9	43.9±3.0	46.8±2.9

TABLE 11B. As in Table 11A with 10-mm-mesh litter bags

Months	Litter bag, aspen	Litter bag, balsam	Surrounding organic matter
12	9.8±4.0	13.1±3.9	44.2±3.0
24	13.2±3.9	11.8±3.9	38.4±3.0
36	48.4±3.0	50.2±2.6	59.4±2.4
48	68.4±2.7	66.2±2.4	73.9±2.4
60	47.8±2.8	44.6±2.9	56.3±2.3

the organic horizon and thus contained leaves in various stages of decomposition (a situation which was verified by fungal isolation data (Visser, personal communication) from leaves held in litter bags for 3, 4, and 5 years)), it was decided to change to a different litter-bag arrangement. There was little visual evidence of faunal comminution of litter confined in the hairnets, and the well-defined L, F, and H layers (Lousier 1974*a*) also indicated no gross comminution or vertical mixing of the litter by soil fauna. Carter (1975) and Mitchell (1974) stressed the absence of large shredding fauna (Lumbricidae, Diplopoda, Pulmonata, dipteran larvae) in the aspen soil and litter. The representatives of these groups that Mitchell (1974) found were generally small species and he described their food habits as 'small-particle' feeding and (or) coprophagous in nature. Thus, it was decided that faunal exclusion would not be a problem for mesh sizes as low as 3 mm because such mesh could still allow the larger species present (e.g., Carabidae) to pass through. The flat, 20 cm × 20 cm, 3-mm-mesh bags used had no leaf drop-out and nestled into the fresh litter well; after 12 months all of these litter bags had been completely covered by the next leaf fall. The leaves in these bags were laid flat, as is most natural leaf litter, and were spread out in a manner similar to natural leaf fall (10.50 g aspen leaves per bag (400 cm^2) approximates to the annual leaf fall (Table 3)). From visual observations of the condition of the leaves, the 'behaviour' of the litter bags and their downward movement through the litter layers and the better moisture regimes inside the litter bags (Table 11), it was concluded that the 3-mm-mesh bags were the better litter-bag arrangement for studying leaf litter decomposition over time in this deciduous woodland.

The tethered leaf results are comparable with those that were obtained by Witkamp and Olsen (1963) and Anderson (1973*b*). Tethered leaves would perhaps be useful in studying the first 12 months of decomposition of robust plant material, but beyond that their usefulness is limited. It is important to check if there are differences in microflora present, colonization rates, and chemical change between tethered and confined material.

There are two methods generally used for litter-bag studies of leaf litter decomposition: (1) a large number of litter bags is set out in the field study plot(s) at the beginning of the project (usually just after maximum leaf fall); at each sampling time, a random sample of litter bags is chosen, oven-dried, and weighed; and (2) several litter bags are placed out in the field study plot(s) at the beginning of the project, retrieved, oven-dried, and weighed at each sampling time, and then replaced in the study plot(s) for further measurements. Method 1 is the most conventional but has, as its major logistic constraint, the need for a large number of litter bags to allow for enough sampling times and enough replication in each sample. Method 2 has been used by some researchers (Birch and Friend 1956; Birch 1958; Drobnik

1961; Witkamp 1966; Stark 1973) and the repeated drying was shown to increase the decomposition of organic matter. However, Suffling and Smith (1974) concluded that repeated artificial drying of old field (herbaceous) litter did not significantly alter decomposition rates. However, this conclusion was derived from an experiment which ran for only 12 weeks. The number of times that different sets of litter were dried were 11, 6, 4, 2, and 1, which seemingly allowed little time for some of the bags to remoisten and equilibrate between sampling times, counteracting any potential effects that drying could initiate.

While seasonal drying of litter in natural conditions, with litter temperatures under 30 °C, may not have a significant effect on organic matter decomposition, repeated cycles of artificial drying of litter at temperatures near or above 80 °C can significantly increase (1.9 times in experiments performed by Jager and Bruins (1975)) the rate of decomposition and could lead to overestimations of dry weight loss in method 2.

Various physicochemical factors, e.g., litter moisture content and pH (Birch 1958; Birch and Friend 1961), have been shown to be important in experiments involving successive cycles of drying of organic matter. Retrieving the same litter bags at each sampling time, replacing them in the study plots after oven-drying, and removing extraneous litter materials obviously disturb the bagged litter and the litter environment surrounding the litter bag in the field. Such disturbance and high-temperature oven-drying destroy the continuity of the microbial succession sequence; over a short experimental period, this could allow limited microbial activity and, consequently, little decomposition. Some of the physicochemical phenomena associated with the release of litter nutrients caused by drying, e.g., hydrolysis, destructive chemical reactions, physical solubilization, and desorption of absorbed matter (Jager and Bruins 1975), could affect more structurally complex tree leaf litter to a greater extent than herbaceous litter when subjected to artificial drying at high temperatures.

3. *Litter Decomposition Models and Accumulation of Soil Organic Matter*

Various authors (Jenny *et al.* 1949; Greenland and Nye 1959; Olsen 1963; Bunnell and Tait 1974; Howard and Howard 1974) have attempted to use mathematical models to describe plant litter decomposition and accumulation of organic matter. The model used by most authors has been the negative exponential function (Olsen 1963), while a model more recently used was an asymptotic regression (Howard and Howard 1974). The difference between these two models is that in exponential decay, the weight remaining tends to zero as time progresses and one can calculate how long it would take for certain percentages of the litter to decompose. However, an asymptotic regression tends to a limiting value as time progresses. Howard and Howard (1974), in their studies on the effects of animal exclusion on rates of litter decomposition, found that an asymptotic regression best fitted their data, and these authors suggested that the limiting values (36–65%) of the regression were due to the absence of fauna, which also indicated that fauna may be more important in some habitats than in others in terms of 'priming' litter and stimulating microbial activity. Despite the good fit obtained with asymptotic regressions over the course of their experimental study, it is doubtful whether this model is applicable for the description of the overall rate of litter decomposition in the field.

The use of the negative exponential function to describe the instantaneous decay rate, k (Olsen 1963), has come under some criticism (Minderman 1968; Anderson 1973*b*). This model implies that decomposition can be represented logarithmically, i.e., k is constant over the course of decomposition. Minderman (1968) concluded from the findings of field decomposition studies that decomposition rates and observed accumulation rates are not accurately described by the negative exponential function. He suggested that while different biochemical components of the litter decompose at different rates and each may conform to the decay model, the overall decomposition rate would be better described by calculating the sum of these exponential regressions; the sum would not necessarily follow the same function. Anderson (1973*b*) supported Minderman's arguments and suggested that dry weight loss as a result of leaching and microbial activity may conform to the negative exponential function in faunal exclusion experiments. However, the evidence of Howard and Howard (1974) did not support this suggestion.

Bunnell and Tait (1974) have modified the negative exponential decay model and have answered some of the criticisms of the model.

They have divided dry weight loss into two components, losses by respiration by microorganisms using the substrate and losses through leaching, and omitted comminution by microflora and microfauna. The leachable component was represented as a 'faster-moving' compound group and the respired component was considered a 'slow-moving' compound group. The higher decomposition rates for the 1st year of decomposition may be attributable mostly to leaching effects (Anderson 1973*b*; Heal and French 1974). The modified equation for total weight loss, as a function of time ($W(t)$) is

$$W(t) = W_1 e^{-r_1 t} + W_2 e^{-r_2 t},$$

where W_1 = the initial weight of the readily leached component, r_1 = average annual weight loss of the readily leached component, W_2 = the initial weight of the less readily decomposable component, the lignocellulose structural fraction, and r_2 = average annual weight loss of the less readily decomposable component.

The best mathematical fit to the above equation would involve no assumptions or theoretical constraints, e.g., compound group W_1 is still assumed to move faster than W_2, but it need not be entirely leached in the 1st year of decomposition. The increased goodness of fit is obtained by fitting a straight line through the data points for years 2, 3, 4, etc. The slope of this line is r_2 and the point of interception on the y-axis is W_2. The rest of the curve is filled in for the first 2 years as is shown in Fig. 4. This portion of the curve is the "total temperature–moisture–respiration response surface," ... "a linear combination of the chemical-specific response surfaces with each chemical-specific response surface contributing in proportion to the amount of that chemical group in the substrate" (Bunnell and Tait 1974) or, more simply, the summation of a number of exponential functions suggested by Minderman (1968).

Figure 4 presents the regression analysis (after Bunnell and Tait 1974) for dry weight loss in aspen and balsam litter over time. For aspen, $W_1 = 23.1\%$, $W_2 = 76.9\%$, 12-month dry weight loss measured = 26.2% (Table 5); for balsam, $W_1 = 21.4\%$, $W_2 = 78.6\%$, 12-month dry weight loss measured = 21.2% (Table 5).

Weight loss of the less decomposable components (W_2) of balsam lagged behind that of aspen over the first 12 months of decomposition. This could account for the significant differences in dry weight loss between aspen and balsam leaf litter over the first 18 months of study (Table 5). However, the litter bags were placed in the field 1 month after litter fall and 1–2 weeks before the autumnal soil freeze, and the more structurally robust balsam leaves may not have had a chance to remoisten and equilibrate (and be colonized as quickly as the aspen leaves) before the extremes of widely fluctuating surface temperatures during soil freezing. Dividing the initial weight of the less readily decomposable fraction (W_2) by $t_{0.99}$ (Table 5) gave values for annual dry weight loss for W_2 (3.2% for aspen and 2.9% for balsam) which compare with the value of about 3% given by Cragg (1969) for the northern Rocky Mountains.

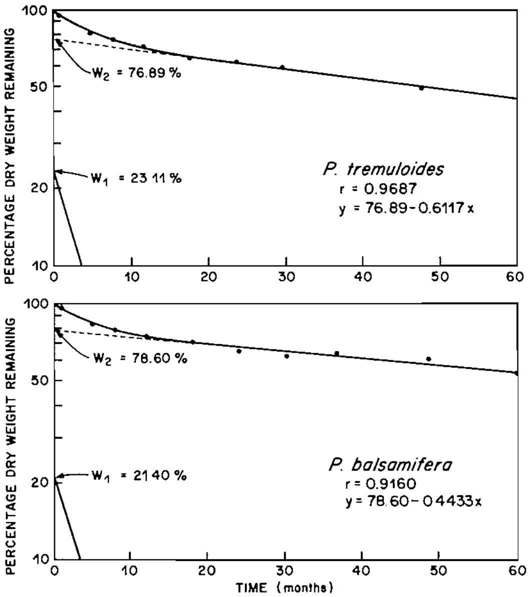

FIG. 4. Dry weight loss from decomposing aspen and balsam leaves: a two-compartment litter decomposition model (after Bunnell and Tait (1974)).

The coefficients of correlation of observed and expected weights remaining were 0.999 for aspen and 0.988 for balsam litter (Fig. 4). Given that the regressions did not include weight losses due to organismic comminution of litter, and given the dearth or absence of litter-shredding fauna in the aspen study area (Mitchell 1974), the *Populus* species decomposition data fit quite well the 'improved' negative exponential decay model of Bunnell and Tait (1974). However, such a good fit may be characteristic of ecosystems with a low annual rate of litter decomposition, in

TABLE 12. Plant biomass, soil organic layer mass, and the percentage of organic matter and carbon contained in each component (weights in kg ha^{-1} × 10^3)

		Organic matter		Carbon content	
	Weight	%	Weight	%	Weight
Vegetation					
Trees	77.1[a]	98	75.6	48	36.3
Roots	33.0[b]	98[b]	32.3	48[b]	15.5
Understory	1.6[c]	94	1.5	46	0.7
Roots	3.2	98[b]	3.1	48[b]	1.5
Total vegetation	114.9		112.5		54.0
Soil					
A_0L	10.6[d]	91	9.6	46	4.4
F	20.9[d]	84	17.6	45	7.9
H	59.5[d]	79	47.0	38	17.9
Ah	48.3[d]	10[e]	4.8	13	0.6
Total soil	139.3		79.0		30.8
Total	254.2		191.5		84.8

[a] Peterson *et al.* (1970).
[b] Percentages from Oslen (1970).
[c] Average for open and closed canopy.
[d] These measurements made just before autumn leaf fall.
[e] Bissett (1975).

which case, the readily leachable component is more easily identified.

The accumulation of organic matter in the A_0 layer is dependent on the rate of litter input and litter decomposition, topography, and the soil moisture and temperature regimes (Tsutsumi 1971). Table 12 illustrates the distribution of organic matter and carbon in the aspen woodland. The share of the litter fall (Table 3) in the total organic matter is 3.7%, which fits the range of 2–4% for older deciduous stands (Rodin and Bazilevich 1967). The total organic matter for deciduous and broad-leaved forest varies from 75 to 150 × 10^3 kg ha^{-1} and in older stands can range as high as 250 × 10^3 kg ha^{-1} (Rodin and Bazilevich 1967). The organic matter mass of 191.5 × 10^3 kg ha^{-1} for the Kananaskis aspen woodland exceeded that (152.4 × 10^3 kg ha^{-1}) for a 50-year-old *P. tremula* forest (Rodin and Bazilevich 1967).

Jenny *et al.* (1949) have shown that if the fractional loss rate (k) is constant and expressed as

$$k = \ln (\text{wt. at time } t/\text{wt. at start})/t,$$

where t is in years, then, in a steady-state system, if I = total annual litter input and X_{ss} = total accumulated organic matter, $k = I/X_{ss}$. In the Kananaskis aspen woodland the values of k calculated from litter-bag losses (Tables 5 and 6) exceeded that calculated from production and accumulation estimates ($I/X_{ss} = 0.093$). Heal and French (1974) attributed such differences to any or all of the following factors: (*i*) overestimation of litter-bag losses; (*ii*) underestimation of production; (*iii*) overestimation of accumulation; (*iv*) declining fractional loss rate (k); (*v*) major environmental changes during the period of accumulation; and (*vi*) the system may not be in steady state. In the present study, it was felt that factors (*ii*), (*iv*), and (*vi*) may be more important, with (*iv*) and (*vi*) probably being the most important. The graphs of weight loss against time (Fig. 4) indicated a loss rate declining with time and Table 13 indicated a loss rate declining with depth. In fact, the values of k determined from litter-bag losses (Tables 5 and 6) tended with time to approach the value of k calculated from I/X_{ss} (0.093).

Some of the above six factors can be tested by means of constant-coefficient models of production, decomposition, and accumulation; for example, the basic steady-state equation

$$dx/dt = I - kX \text{ (Olsen 1963)},$$

where I = organic matter input, X = organic matter accumulated, t = time, and k = the decomposition constant. By using k values derived from the litter bags, the calculated amount of organic matter accumulated was underestimated in comparison with observed values (e.g., after

TABLE 13. Distribution and turnover of carbon during the course of 99% decomposition of an annual increment of aboveground litter carbon (all weights in kg $ha^{-1} \times 10^3$)

Layer	Accumulation of litter carbon	Residence time of litter in each layer, year	Amount of carbon lost during residence time in layer	Standing crop of total carbon in layer	Residual carbon
L_1 (current litter)	2.02	1	0.53		
L_2 (old litter)	3.87	3	0.36	4.43	0.56
F (fermentation)	2.73	3	0.32	7.89	5.16
H/Ah (humus and black mineral soil)	5.71	18	0.79	18.48	12.77

TABLE 14. Distribution of the residual carbon in each of the litter and soil layers (all figures in kg $ha^{-1} \times 10^3$)

Layer	Residual carbon	Root carbon	Fungal carbon	Bacterial carbon	Other carbon
L_2	0.56		0.062	0.003	0.495
F	5.16	0.55	0.21	0.08	4.32
H/Ah	12.77	1.01	0.26	0.03	11.47

3 years, $X_{CALC} = 8460$ kg ha^{-1}, $X_{OBS} = 9630$ kg ha^{-1}; after 6 years, $X_{CALC} = 21\,310$ kg ha^{-1}, $X_{OBS} = 27\,160$ kg ha^{-1}; after 24 years, $X_{CALC} = 24\,910$ kg ha^{-1}, $X_{OBS} = 78\,970$ kg ha^{-1}). It was not known what portion of this underestimate was attributable to problems inherent in the methodology used in this study or what portion was because of non-steady-state conditions.

The carbon present in the soil layers has various sources, the most important of which is, of course, annual litter fall. However, there are other essential sources, i.e., live and dead plant roots, microflora, aboveground and belowground fauna, and faecal material. Because the soil community involves a complexity of feeding relationships, the carbon assimilated does not always come directly from the standing crop of litter carbon. The dynamics of carbon turnover in one population of soil organisms depend on the population's feeding habits, growth and metabolic rates, annual and seasonal abundance, generation time, and intrapopulation and interpopulation competition. The microflora and Protozoa, with field generation times ranging from a few hours (Stout 1973; Parinkina 1974; Miller and Laursen 1974) to a few days (Gray *et al.* 1974; Lousier 1974*a*, 1974*b*), will have a greater role in carbon cycling in the aspen woodland than will those organisms with lower densities and longer generation times, e.g., 0.5–1 year for Enchytraeidae (Dash and Cragg 1972*b*) and 4.2 years for Oribatidae (Mitchell 1974).

Table 13 follows an annual increment of carbon from aboveground litter input (Table 3) through to 99% decomposition, with calculations of the amount of litter carbon accumulated in each organic layer and the dry weight loss of carbon at each stage of decomposition. Using the figure of 202 g C m^{-2} as the annual increment involved the assumption of 21% non-leaf tree litter (Table 3). If the ratio of non-leaf to leaf litter is higher, then using 202 g C m^{-2} will provide only minimum estimates of accumulation and release of carbon by the decomposition process. Increasing the amount of the annual increment will simply increase the estimates of accumulation and release of carbon (from the measured standing crop of carbon in the old litter (L_2 = 443 g C m^{-2}) and the decomposition rates from the regression (Fig. 4); it appears that the real annual increment of carbon is about 225 g m^{-2}, which gives a non-leaf litter carbon input of 31%). The amount of litter carbon accumulated in the L layer was 87% of the measured standing crop of carbon, in the F layer it was 35%, and in the H layer it was 31%. By using root biomass estimates (K. Krauter, personal communication) and fungal (Visser and Parkinson 1975*a*) and bacterial (M. J. Elliott, personal communication) biomass estimates, a portion of the residual carbon can be accounted for (12% in L, 16% in F, and 10% in H and Ah) (Table 14). However, there is still a large amount of residual carbon remaining, the major sources of which would include humic materials, the living and dead roots unaccounted for, other microorganisms, invertebrates, invertebrate faeces, and dead soil organisms.

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